

PRESIDENTIAL ADDRESS TO THE TENTH ANNUAL  
MEETING OF THE LEPIDOPTERISTS' SOCIETY

Ladies and gentlemen:

To my great regret it is not possible for me to be present at your meeting, since I was in the United States only this past summer, at which time I was able to visit the meeting of the Pacific Coast Section of our society. I can, therefore, only send you this presidential address, together with my best wishes for the success of this meeting.

Again and again I note in conversation with lepidopterists that very unclear views exist concerning the systematic categories, especially among those who pursue the study of butterflies and moths as a hobby while earning their living at a very different occupation. Permit me, then, for this reason to say a few words on the subject, even if they hold little that is new for the specialist.

The smallest systematic unit is the *individual*. The assemblage of individuals of one species in a definite, circumscribed area of greater or lesser extent forms the *population*. The concept of the population may be used in various ways. One may speak of the population of a field or a forest, but one may speak also of the population of a mountain or of a country, if the species concerned is widely distributed and varies little or not at all. In numerous cases where the species occurs only in very restricted habitats — biotopes — and hence is found throughout its range in a more or less spotty or island-like distribution, the inhabitants of each such small territory are considered to make up a population. As a rule a population is genetically uniform and hence belongs to a single subspecies, but in some instances a population can be comprised also of individuals of two different subspecies of the same species, living together, as will be shown later.

Also within a single population we often find individuals which differ considerably in appearance from one another. This observation leads us to the problem of *variation*. In this connection, we note that among individuals closely related to one another we may encounter certain ones, *variants*, of strikingly different appearance. There exists, therefore, *variability*. This variability can have very different causes. In many instances we find a more or less considerable amount of hereditary individual variability. In extreme cases the descendents of a single parental pair can be so different among themselves that no two

of them are alike as, for example, in *Euphydryas aurinia* Rott. In contrast, the widely distributed palæarctic Brimstone (*Gonepteryx rhamni* L.) may be mentioned, among specimens of which hardly any difference at all may be discerned. The spread or scatter of normal variability in a species is termed its *range of variation*, and one may apply the term to the entire external appearance (habitus, gross external facies) as well as to particular characters only, such as the form of the valva or of the uncus in the male genitalia. Individuals lying outside the normal range of variation either of a particular character or of the entire habitus are termed *extreme variants*. *Aberrations*, however, are pathological individuals which, because of a genetic defect or endocrine disturbances or even external influence during the time of their development, show a morbidly changed appearance. Thus dwarfs can result from insufficient food during their larval stage, but they may also arise because of irregularities in the endocrine system. Not rarely one encounters suddenly in a population a completely new form which sometimes in the course of succeeding generations becomes increasingly common. This sudden occurrence of a new form arises from an alteration in the genetic constitution—from a *mutation*. Most mutations bring with them a reduction in vigor in the affected individual and the form disappears rapidly. Many are only recessively transmitted but some, however, are dominant and have thereby a definite selective disadvantage. There are instances where a population in the course of time becomes comprised only of individuals of the newly arisen form. A form which occurs as a result or consequence of a mutation is termed a *mutant*.

Individual variability within a population can be purely genetic in nature or it can be induced by external factors, though indeed the ability of particular external influences to act in a particular way is likewise determined by heredity. The external appearance of a butterfly adult, and under certain circumstances also of the early stages, is commonly strongly influenced by external, mostly climatic, factors. In some species members of a single population in successive years of different weather conditions can be strikingly different as for example the Kite Swallowtail (*Graphium podalirius* L.) in middle Europe in hot and cool years. Even comparatively limited microclimatic differences not infrequently can leave their mark in the habitus of a butterfly. For example, within the genetically certainly quite uniform Upper Bavarian populations of the blue, *Plebejus argus* L., the lighter colored form *uliginosa* Dannehl is encountered only in the wettest parts of the bogs. By the action of external factors, often apparently by the influence of day length on the

early stages, or through the alternation of wet and dry seasons, the different generations of a species encountered during the course of the year are commonly more or less different: *seasonal dimorphism*, observable in an especially pronounced degree in the middle European *Araschnia levana* L. with its summer form "prorsa". In middle Europe up to three generations, mostly more or less differing from one another, can be found in individual species, designated as *spring form* (*generatio vernalis*), *summer form* (*generatio æstivalis*), and *fall form* (*generatio autumnalis*). In warmer lands the generations of many species follow one another without showing discernible differences.

In many cases it is exceedingly difficult, indeed often almost impossible, to determine whether one has to do with genetic or nongenetic variability, since the relations between internal (genetic) factors and those operating from the outside, one sometimes reinforcing the other, sometimes working against the other, are enormously complicated. Only extensive breeding and hybridization experiments, under the most varied conditions, can bring understanding here, but such experiments, for obvious reasons, can be carried out only very infrequently.

Apart from examples of variability discussed so far the members of a single population in some instances may have a very diverse appearance. Almost always the sexes are more less different in habitus as is well marked, for example, in the blues (*Lycænidae*). This is termed *sexual dichroism*. Also within a single sex two or even more genetic forms may be encountered, occurring together in the same population. In such cases we speak of *dimorphic* or *polymorphic species*, depending on whether two or more than two forms are involved. Examples of such dimorphism in one sex are *Argynnis paphia* L. with its female form "valesina" or those species of the genus *Colias* which have white females along with those "normally" colored (yellow, orange or red).

Populations differing from other populations of the same subspecies, or groups of populations standing closer to one another than to other populations of the same subspecies are termed *local forms*.

The next higher category is the *subspecies*. It is a complex of individuals of the same phylogenetic origin, genotypically and structurally fundamentally uniform though often strongly variable phenotypically, and completely fertile among themselves. It is quite possible, then, for individuals differing greatly in appearance to belong to the same subspecies. In connection with this variability we need recall only the *ecological forms* found in many subspecies, such as the *altitudinal forms* (*formæ altæ* or, at very high elevations, *formæ altissimæ*). Some species,

indeed, are represented in mountainous regions by genetically fixed subspecies which have characters of the same sort as those of ecological altitudinal forms. It is usually very difficult in such cases to determine whether an endemic subspecies is involved or only an altitudinal form of a more widely distributed subspecies.

Subspecies arise through the isolation of a larger or smaller number of populations of a species in the course of geologic history. They are conceived of as potential species. The middle European subspecies owe their origin, for example, to the several changes of area caused by the Pleistocene glaciations, to the secondary intermingling of forms already genetically differentiated and to altered living conditions.

*Geographical, biological and physiological subspecies* may be distinguished. The commonest, that is the most frequently observed, kind is the *geographic subspecies*. The majority of species are composed of subspecies more or less genetically (and hence usually morphologically) differentiated, whose ranges are normally mutually exclusive (allopatric). The boundary areas often show a zone of intergradation of greater or lesser width, across which one sees a gradual change from one to the other. Gradual changes with respect to one or several characters are termed *clines*. To be sure, this term states nothing concerning the origin of this variational series. In some instances the terms *subspecies* and *cline* are identical, specifically if a subspecies shows within its range a gradual transition in one or several characters. Should such a gradual change in characters extend across the territory of two or more subspecies, then the whole complex would be termed a cline. Geographically neighboring subspecies are usually perfectly fertile *inter se*; those more widely separated need not be so. These may behave as species and, if in the course of their distributional history they should meet somewhere again they would then live side by side as two species, without intermixture.

*Biological subspecies*, which do not need to be differentiable on the basis of pattern or structure, are isolated by differences in their manner of living, commonly also by having different flight periods. They may occupy the same area with another subspecies of the same species (be *sympatric* with it). The same is true of *physiological subspecies*, which may be so strongly differentiated from each other by differences in secretions (such as different sex odors) or by differences in chromosome structure that successful crossing of the two, even though they be *sympatric*, has become impossible. Biological and physiological subspecies occur not rarely in the Lepidoptera. In contrast to geographic subspecies, however, very little attention has as yet been devoted to them.

These kinds of subspecies, geographical, biological and physiological, are, naturally, susceptible to all the forms of variability already discussed in connection with the population.

The *species*, the next higher systematic category, consists usually of a series of subspecies. Only a few species are not divided into subspecies and thus, over their whole range, subject only to individual and ecological variation. Here we must make a distinction between monotypic species that are widely distributed and those occurring only in very small areas. These latter not infrequently were at one time much more widespread and probably also divided into subspecies, though today they occur only as relicts in limited areas. The division into subspecies has originated in the course of the evolutionary history of the particular species. In simple cases the species consists of a series of geographically more or less mutually excluding subspecies. As a rule, however, the subdivision of a species is not so simple. Along with geographical subspecies and their local forms and ecologically conditioned forms occur the biological and physiological subspecies, two or more of which on occasion may occur in the same area. The species, therefore, is usually an extraordinarily complicated structure. Further, subspecies can have diversified to such an extent that in many instances it is difficult or impossible to determine whether they are subspecies or already distinct species. In species with numerous subspecies and large distribution areas neighboring geographic subspecies are usually interfertile and commonly even form clines; terminal members, however, as already mentioned, often are no longer capable of interbreeding and behave as species. For species which are made up of a series of geographically mutually excluding subspecies the terms "*Formenkreis*" (circle of forms), "*Rassenkreis*" (circle of races) or "*Rassenkette*" (chain of races) were proposed, though without any implication that they represented another systematic category. Among the subspecies of a *formenkreis*, in some cases it is not possible to determine exactly whether we have to do with subspecies or with full species. The systematic category "species" is therefore not sharply distinguishable from the category "subspecies," for if we assume a natural, continuing evolutionary development all transitional stages must exist between subspecies and species. Where the boundary should be drawn here, and for the proper order of the system this is necessary, must in each case be left to the more or less subjective judgement of the systematist involved. Since all forms encountered in nature are in a state of continuing development our view can therefore give only a cross-section of the state of development at a single moment and it is obvious

that we encounter the various forms in all stages of evolution, making their arrangement into an orderly plan—the hierarchy of systematic categories—extremely difficult. It is for these reasons that in all work in the field of systematics, and especially in the evaluation of systematic conclusions it must be remembered that this absolutely necessary taxonomic ordering can only be produced: that we are obliged more or less to force into a system what in nature had no such system. Moreover, as already mentioned, in the consideration of the animal kingdom of to-day we do not have their phylogenetic tree before us, but merely a cross-section, intersecting the present day groups and forms in the current state of their development. We should never say, therefore, that a particular recent group (or species, subspecies, etc.) is derived from another recent group; far more likely is it that both have been derived from a common stem. Commonly, however, one of the two has evolved more rapidly than the other (that is *apomorphic*) while the other, in spite of having had the same length of time available to it, has evolved less from the common ancestral group (species, etc.) and is, therefore, *plesiomorphic*. This explains why the so-called “primitive” groups are encountered in the most different places in the present system.

After this very theoretical digression let us return to the problem of the *genus*, a systematic category under which closely related species are united, species which, according to their phylogenetic history, belong together. Generic grouping as applied today is far from uniform, varying according to the state of research in the particular group. Large genera which one cannot divide into subgenera are most often a sign of deficient study of the group. In some genera the species exclude one another geographically, analogous to the geographical subspecies of a *Rassenkreis*. In such cases one has a *genus geographicum*, that is to say a higher and phylogenetically older stage of a *Formenkreis*, in which the several subspecies have attained species rank.

I hope that I have not bored you too much with these remarks. I know that for many — perhaps most — of you I will have said little that is new. In closing I wish your meeting to be both agreeable and harmonious and express once more my regret that I cannot be with you in person.

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